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Life history baseline of unexploited populations: The case of *Beryx splendens* from the Sierra Leone Rise

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ABSTRACT

This study examines for the first time the biology of alfonsino (*Beryx splendens*) from three small seamounts of the Sierra Leone Rise (SLR), an unexploited and fragile ecosystem in the Atlantic, using data from an experimental survey carried out in 2001 by Spanish longliners. In general, the lack of rigorous baseline data limits the implementation of efficient management and conservation plans in fisheries strategies. Therefore, the main aim of present study was to provide baseline information on basic biological parameters of the alfonsino population associated with an unexploited ecosystem. A total of 17296 individuals of alfonsino were sampled from SLR. Alfonsino is gonochoric and presented an unbalanced sex ratio, there were significantly more females than males. Taking into account the results in stage of maturity of alfonsino and the gonadosomatic index values during studied period, we can conclude that at least one reproductive period in these seamounts was in the late spring and early summer. The spawning stage was attained at a minimum fork length of 23 and 25 cm for males and females, respectively. The size at which 50% of the population attains sexual maturity was approximately 28 and 27 cm for males and females, respectively. The stock structure of alfonsino showed a segregation of the size with the depth, as they increase in size they move into the deeper water.

1. Introduction

Beryx splendens Lowe, 1834 (named with the vernacular name of alfonsino) is one of the best-known representatives of 'seamount-aggregating fishes' (Shotton, 2016; Koslow et al., 2000; Morato et al., 2006), inhabiting seamounts or canyons in tropical, subtropical and temperate waters around the world, excluding the Northeastern Pacific (Busakhin, 1982; Vinnichenko, 1996; Menezes et al., 2009). Its life cycle occurs in geographically distant areas (Alekseev et al., 1986; Lehodey et al., 1997). Thus, mature individuals migrate to reproductive areas through current systems and meso-scale eddies (Alekseev et al., 1986). In the North Atlantic, the alfonsino population is mainly associated with the subtropical eddies (Alekseev et al., 1986). Moreover, alfonsino is able to stay in the Oxygen Minimum Zone (OMZ) and migrate through it Saavedra et al. (2015). Alfonsino forms aggregations that are commercially valuable over seamounts around the world (Clark, 2009; Froese and Sampang, 2004). In European waters, alfonsino is considered as a bycatch species in longline mixed fisheries (Castro et al., 2011; ICES, 2010). However, in the Macaronesian area it is one of the targeted species of a traditional demersal fishery (Pinho and Menezes, 2005, 2009; Menezes et al., 2006), being marketed fresh in the whole archipelago (Rico et al., 2001).

Seamounts can be a crucial habitat for fishable species that form aggregations for spawning or feeding (Clark, 2001). Seamounts have been or may become fishing areas (Bergstad et al., 2019). In general 'Seamount Aggregating Fishes' (SAF) show low yield in fisheries, for this reason, SAF are susceptible to overfishing (Booth and Buxton, 1997; Clark et al., 2016), and they show a low limit to the large-scale exploitation fishery (Koslow et al., 2000; Cheung et al., 2007). The Instituto Español de Oceanografía carried out an experimental fishery survey (named PALGUINEA2001) to prospect for a new zone for Spanish bottom longliners in international waters from SLR between January and July 2001 (for major details, Salmerón et al., 2015). In this context, Salmerón et al. (2015) observed a rapid depletion yield in

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alfonsino fisheries from the Sierra Leona Rise during the experimental survey that lasted seven month. According to the previous literature and a bibliographic intensive search we did not find evidences for a previous exploitation from this fishing ground.

There are many evidences on life history changes in commercially exploited fish stocks (Heino and Dieckmann, 2008; Sharpe and Hendry, 2009). In general, the lack of rigorous baseline data limits the implementation of efficient management and conservation plans in fisheries strategies (Garrabou et al., 2017). For this reason, it is important to establish baseline knowledge on the life history of unexploited populations from fisheries management point of view (Claudet et al., 2010). Therefore, the main aim of present study was to show the baseline of basic biological parameters of the alfonsino population associated with an unexploited ecosystem, based on the scientific data collected from this experimental fishery survey.

2. Materials and methods

2.1. Study area and fishing gear

In the Eastern Central Atlantic, a chain of about ten volcanic seamounts forms the Sierra Leone Rise (Hekinian et al., 1978; Pakhorukov, 1999). The study area comprised three fishable seamounts within the Sierra Leone Rise (SLR) (9.01°–5.6°N and 19.83–26.93°W) (Fig. 1): Falsos sureste (FS) with a summit depth of 485 m, Machucambo (MA) with a summit depth of 280 m, both in the north part of the Sierra Leona Rise and Rompetodo (RO) with a summit depth of 280 m located in the South. The area is a cyclonic region crossed by several seasonally changing zonal jets (Stramma and Schott, 1999; Rosell-Fieschi et al., 2015) encircled by the westward North Equatorial Current and the eastward North Equatorial Countercurrent (NECC). An important feature is an oceanic thermal upwelling dome in the northeastern tropical Atlantic, which is known as either the Dakar Dome or the Guinea Dome (GD) (Rossignol and Meyrueis, 1964; Mazeika, 1967), which is occupied by the inner part of the North Atlantic Tropical Gyre, centered at about 10°N and 20°W (Siedler et al., 1992); the GD intensifies in summer as a result of the northward penetration of the Inter-Tropical Convergence Zone (ITCZ) and the South Atlantic High, bringing westward winds, surface water divergence and upwelling (Pelegrí and Peña Izquierdo, 2015).

The previously mentioned experimental fisheries survey (named PALGUINEA2001), was conducted by four commercial longliners (length 23–27 m; GRT56–98 tonnes) that fished together in the Sierra Leone Rise area. Fisheries covered a bathymetric range from 200 to 900 m (for major details, Salmerón et al., 2015)

The longline gear consisted of a monofilament mainline of 2.88–4.80 km in length, with hooks (size 8) placed on branch lines attached to the mainline at intervals of approximately 1.8 m. The longline was suspended over the seabed by buoys and weighed down with small rocks at intervals of 50 hooks. All fishing operations were carried out during daytime; gear was set at sunrise and allowed to soak a minimum of three hours before hauling back onboard.

2.2. Biological sampling

A total of 17 296 individuals of alfonsino were sampled (13 043 in MA, 1325 in RO and 2928 in FS). All individuals were sexed macroscopically and measured to fork length (FL) with accuracy to the lower centimeter. On board a subsample of 3594 fishes were weighted (W, g) and in 424 individuals were assigned the maturity stage. Moreover, a subsample of 1816 individuals was frozen onboard for study in the laboratory. In the laboratory, fork length (FL, to the nearest mm), total mass (W, g), gutted weight (EW, g), sex and gonad mass (GM, 0.01 g) was obtained.

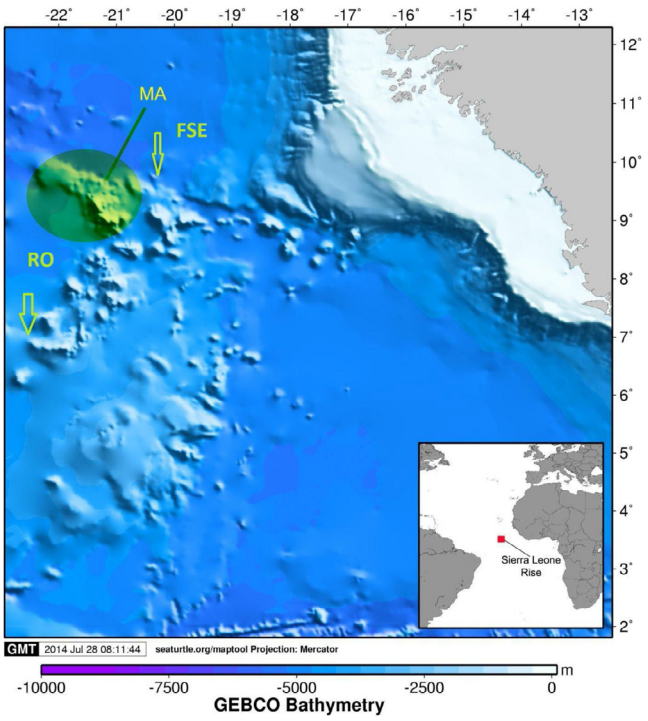

Fig. 1. Location of Sierra Leone Rise and three seamounts Machucambo (MA), Rompetodo (RO) and Falsos Sureste (FS) where this study was focused. Coordinates: 9.01°–5.6°N and 19.83–26.93°W, 200–926 m in depth.

The gonads of alfonsino were observed macroscopically and assigned to a maturity stage among from 1 to 4, according to the recommendations ICES-Workshop on Sexual Maturity Staging of Hake and Monk (ICES, 2007): 1 (immature); 2 (maturing); 3 (spawning) and 4 (post-spawning).

2.3. Data analysis

2.3.1. Length frequency distributions

Length frequency distributions by sex and seamount were developed. Tests for normality were conducted using a Kolmogorov–Smirnov test. In addition, we performed a non-parametric Mann–Whitney U test to compare two variables between the sexes and Kruskal–Wallis test to contrast the sexes among seamounts. All statistical analyses were considered significant at 1% ($P<0.01$).

2.3.2. Sex-ratio

In a similar way to González et al. (2003), the sex ratio (males:females) was calculated grouping the individuals in different segments by 2-cm (i.e. size class) by seamount. Therefore, the males:females ratios were compared to a balanced sex ratio (1:1) using a χ^2 test.

2.3.3. Length–weight relationships

Fork lengths (FL) and body weights (W) were fitted for males and females by seamount separately. Length–weight relationships between W and FL, $W = a\ ^*FL^b$, was converted into its logarithmic expression: $lgW = lga + b\ ^*\ lgFL$.

The parameters "a" (allometric constant) and "b" (shape) were calculated by least-squares regression (Froese, 2006), as was the coefficient of determination (r^2).

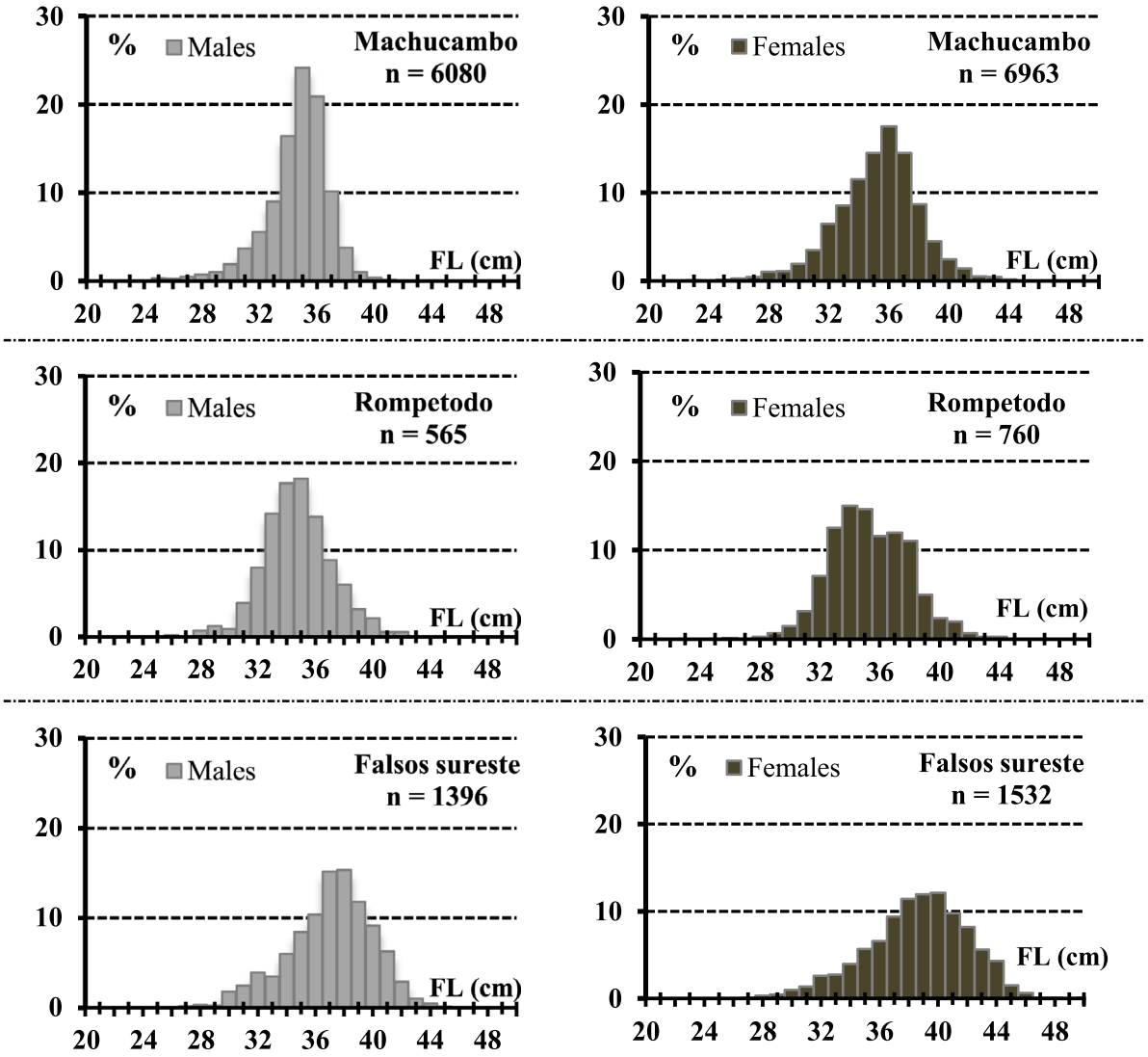

Fig. 2. Length–frequency of distribution of the individuals of *Beryx splendens* sampled from the Sierra Leone Rise (Total Zone, all seamounts together), Machucambo and Falsos sureste, both seamounts in the North of SLR, and Rompetodo in the South of the SLR. FL = fork-length (cm). *Y*-axis in %.

In a first step, we made a first fit of the data, to detect outliers. We remove 4% of the data outliers from the function setting. Posteriorly, we fitted again a new function without these outliers of all individuals by sex and seamount.

Statistical methods used for processed data include calculations of means and standard deviations. Significant differences of b values from 3, which represents isometric growth, was tested with Student t-test (Froese et al., 2011). To test for possible significant differences between sexes, analysis of covariance (ANCOVA) was used.

2.3.4. Le Cren Condition Index, LCCI

The relative condition index was used to assess fish condition. This index was also recommended by the ICES Working Group of Fish Condition (ICES, 2016) and is calculated as follows:

LCCI = W/We

where W is the observed weight per fish and "We" is the expected weight derived from the formula $W = a * FL^b$.

This index allows one to detect weight deviations of a certain length from the expected weight calculated from the species growth curve; values higher than 1, should indicate better nutritional condition and lower values would reflect a poorer condition.

Statistical comparisons between sexes by seamount and among sexes and seamounts were performed using a non-parametric analysis of the variance Kruskal–Wallis and a post hoc U de Mann–Whitney test.

2.3.5. The reproductive period

The reproductive period was determined analyzing the temporal evolution of the gonadosomatic index (GSI) values calculated as:

GSI = 100 ∗ (gonad mass/gutted weight), both in grams

2.3.6. Size at sexual maturity

The size at sexual maturity (length at which the 50% of the fish population reaches maturity) was determined with a non-parametric bootstrap approach, using an automatic routine in the R environment (R Development Core Team. 2015. https://www.rproject.org) called INBIO (Sampedro et al., 2005).

This routine compares number of immatures (stage 1) versus number of matures (stage 2, stage 3 and stage 4) during the available months.

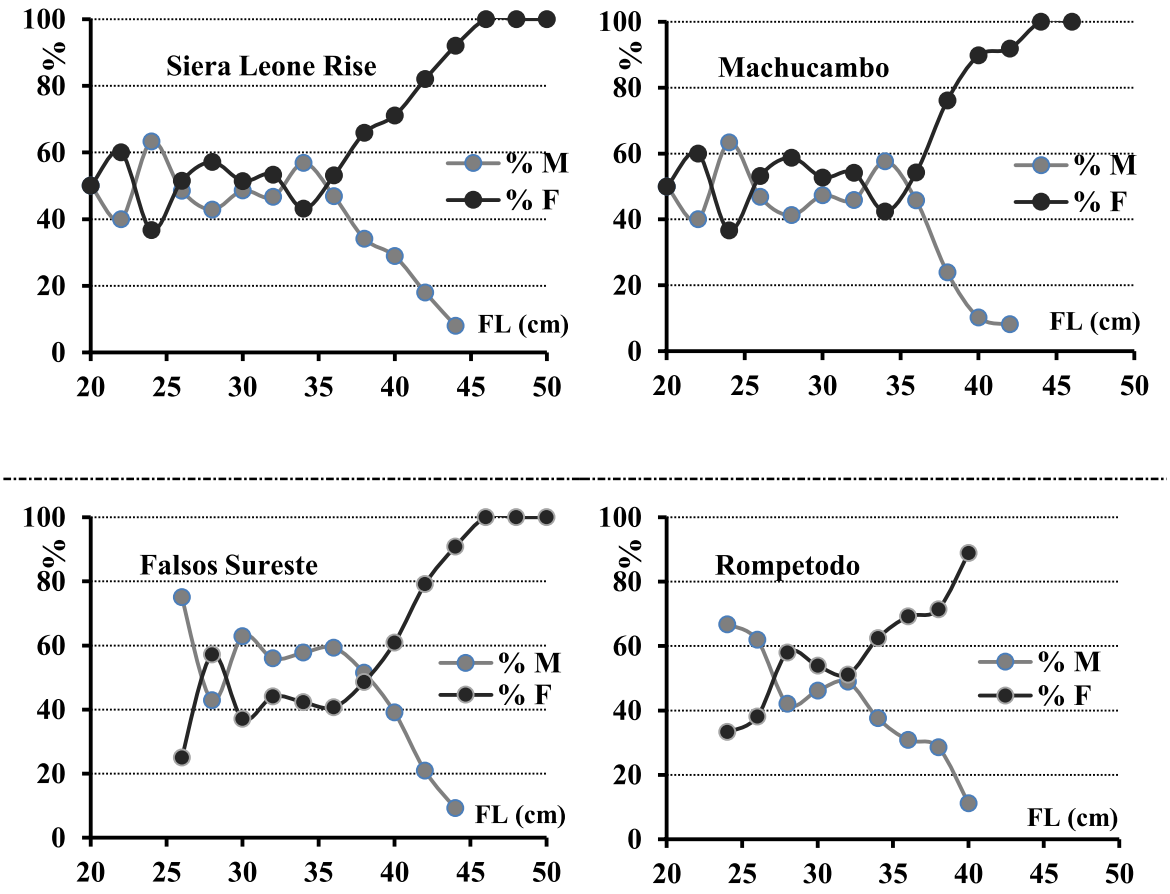

Fig. 3. Sex ratio % of males (M) and females (F) by size class in the whole zone, Sierra Leone Rise and by seamount sampled.

3. Results

3.1. Length frequency

A total of 17 296 alfonsino individuals were sexed and measured off the Sierra Leone Rise, including 8041 males and 9255 females. A wide size-range was recorded, ranging between 20 and 50 cm fork length (FL) for females and between 21 and 45 cm FL for males (Fig. 2 and Table 1). Length–frequency distributions of alfonsino in the area, seamount and sex showed a non-normal distribution (Table 2). There were significant differences in length frequency distribution among seamounts (Kruskal–Wallis test: x2 2016; p (<0.01) as well as between sex in every seamount (Mann–Whitney U test: SLR z: −17.2, $p < 0.01$; MA z: −15.2, $p < 0.01$; FS z: −13.2, $p < 0.01$; RO z: −3.8, $p < 0.01$).

The median value of the FL in SLR was 35 cm. However, shallow seamounts (MA and RO) showed a median values of FL lower than the deepest one (FS), 35 and 38 cm FL, respectively. In fact, the larger sizes were found in FS, with a median of FL of 37 and 39 cm for males and females, respectively. In all sampled seamounts females always presented larger median value than males. In the shallow seamounts, the median of FL was slightly lower in the South (34/35 cm) than in the North (35/36 cm, males/females). Maximum length was found in FS-seamount (45 and 50 cm for males and females, respectively) (Table 1).

3.2. Sex ratio

Females of alfonsino were more abundant than males, they represented around the 53% of the individuals examined from Sierra Leone Rise (SLR) during the survey. Considering the whole area, the sex ratio was significantly unbalanced, 1:1.15 (males:females) ($p < 0.05$) (Table 3).

Table 1
Number of total individuals, males and females; Median value, 25th percentile (Q1), 75th percentile (Q3), minimum and maximum fork length (cm) for in Sierra Leone Rise; Machucambo; Rompetodo and Falsos sureste.

Seamount	Sex	N	Median FL	Q1	Q3	Min FL	Max FL
Sierra Leone Rise	Total	17 296	35	34	37	20	50
	Males	8041	35	34	36	21	45
	Females	9255	36	34	38	20	50
Machucambo	Total	13 043	35	34	36	20	47
	Males	6080	35	34	36	21	43
	Females	6963	36	34	37	20	47
Rompetodo	Total	1325	35	33	37	26	43
	Males	565	34	33	36	26	42
	Females	760	35	33	37	26	43
Falsos sureste	Total	2928	38	36	40	27	50
	Males	1396	37	35	39	27	45
	Females	1532	39	37	41	27	50

The percentage of males and females in the total area and by seamount are shown as a function of size classes in Table 3 and Fig. 3, there were more females than males in all size classes, except in the size class 24 and 35 cm FL and it is very clear that females are consistently larger than males.

In the North, in Machucambo (MA) and Falsos sureste (FS) seamounts, males represented around 47% of the sampled individuals, slightly higher than in the South (Rompetodo, RO) where they were about a 43% of the population. The overall ratio between males and females was 1:1.1 in the North and 1:1.35 in the South. In the shallow seamounts MA and RO, females were dominant in all size classes, with the exception the 26 and 34 cm

Table 2
Tests of normality (Kolmogorov–Smirnov test).

Seamount	N	max D	K-S (p)
Sierra Leone Rise	17 296	0,101	p < ,01
Machucambo	13 043	0,133	p < ,01
Rompetodo	1325	0,103	p < ,01
Falsos sureste	2928	0,090	p < ,01
SLR males	8041	0,127	p < ,01
SLR females	9255	0,091	p < ,01
MA males	6080	0,171	p < ,01
Ma females	6963	0,111	p < ,01
RO males	565	0,115	p < ,01
RO females	760	0,095	p < ,01
FS males	1396	0,121	p < ,01
FS females	1532	0,090	p < ,01

of FL intervals in MA. Contrarily, in the deeper seamount (Falsos sureste, FS) males were dominant up to the large size classes (all below 40 cm in FL) where the tendency reversed.

3.3. Length–weight Relationship

The parameters of length–weight relationship (LWR) by sex and seamount are shown in Table 4. In the case of males, 'b' ranged between 2.84 and 2.86, while in females it was 2.83–2.87. The calculated b for the LWR indicated negative allometric growth (Student t test, t in Table 4). Therefore, alfonsino in SLR acquired lesser weight than cube of its length (allometry negative). The regression models showed that there were no significant differences between observed and predicted growth patterns in males and females (ANCOVA, $P > 0.05$).

3.4. Relative body condition index: Le Cren Condition Index, LCCI

To estimate the physical condition index we used 5274 pairs of length–weight data based on alfonsino caught in different seamounts during the survey (3096 in MA; 1349 in FS and 829 in RO), 136 pairs of length–weight were outliers. The median of LCCI in SLR was 1.00 and 0.99 (standard deviation 0.08) for males and females, respectively, ranging between 0.97 in males of RO and 1.01 in females of RO (Fig. 4). The condition for males and females was not significantly different in the whole zone (SLR) and MA ($p > 0.01$). However, there were significant differences in condition between sexes in FS and RO ($p<0.01$). Males in FS were in better condition than females, whereas in RO females presented better condition than males.

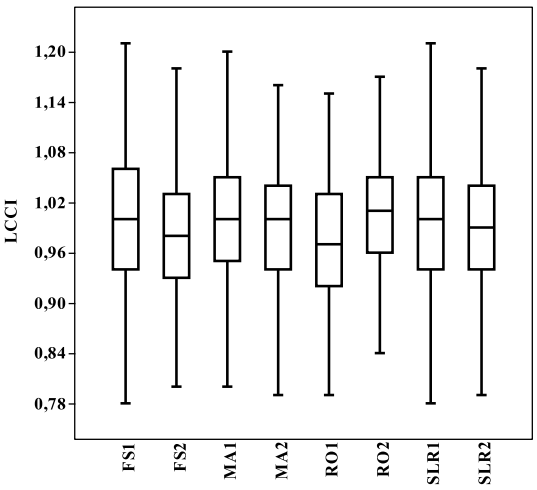

Fig. 4. Box plot (square inside the box, median, 25th to 75th percentile and I 1%–99%) of Le Cren Condition Index (LCCI) of *Beryx splendens* in the Sierra Leone Rise (1 and 2 in the abbreviations of the x axis correspond to males and females, respectively) (FS: Falsos sureste; MA: Machucambo; RO: Rompetodo; SLR: Sierra Leone Rise).

3.5. The reproductive period

3.5.1. Gonadosomatic Index (GSI)

The monthly average of GSI in the area of SLR showed lower values (1.5−1.6) in winter (February–March) increasing to a maximum (4.6) in June to then decreasing in July.

Looking at each seamount separately, we observed that the highest GSI values in MA occurred in spring for both sexes, peaking over April (3.3 for males and 3.1 for females). After this month, a gradual decrease was observed for both sexes. However, while this decrease was observed until the end of the sampling period for males (values around 1 in July), for females the decrease was generally lower and then occurred only until June, to display higher GSI values again in July (around 2). However, in RO the highest values of the GSI were registered in early summer, and a steep increase in the index was observed both for males and females from February (1.6/1.1) to July (5.6/4.1). Finally, in FS seamount, the highest values of GSI were also recorded in early summer, peaking over June in males and July in females. In this seamount, the values of GSI were in general higher than in the other seamounts of the zone, especially in males, which reached

Table 3
Number of males (M) and females (F), Sex-ratio and $\chi 2$ test for *Beryx splendens* in Sierra Leone Rise (SLR); Machucambo (MA); Rompetodo (RO) and Falsos sureste (FS).

Size class (cm)	SLR				MA				RO				FS			
	M	F	Sex ratio	$\chi 2$	M	F	Sex ratio	$\chi 2$	M	F	Sex ratio	$\chi 2$	M	F	Sex ratio	$\chi 2$
20–21	1	1	1:1.00	0,157	1	1	1:1.00	0,157								
22–23	4	6	1:1.50	0,002	4	6	1:1.50	0,002								
24–25	19	11	1:0.58	0,000	19	11	1:0.58	0,000								
26–27	49	52	1:1.06	0,000	44	50	1:1.14	0,000	2	1	1:0.50	0,083	3	1	1:0.33	0,046
28–29	126	168	1:1.33	0,000	104	148	1:1.42	0,000	13	8	1:0.62	0,000	9	12	1:1.33	0,000
30–31	430	455	1:1.06	0,000	340	379	1:1.11	0,000	29	40	1:1.38	0,000	61	36	1:0.59	0,000
32–33	1121	1282	1:1.14	0,000	886	1047	1:1.18	0,000	131	153	1:1.17	0,000	104	82	1:0.79	0,000
34–35	2886	2190	1:0.76	0,000	2468	1816	1:0.74	0,000	216	226	1:1.05	0,000	202	148	1:0.73	0,000
36–37	2361	2671	1:1.13	0,000	1888	2233	1:1.18	0,000	116	193	1:1.66	0,000	357	245	1:0.69	0,000
38–39	713	1377	1:1.93	0,000	289	918	1:3.18	0,000	45	101	1:2.24	0,000	379	358	1:0.94	0,000
40–41	259	637	1:2.46	0,000	31	271	1:8.74	0,000	12	30	1:2.50	0,000	216	336	1:1.56	0,000
42–43	63	287	1:4.56	0,000	6	67	1:11.17	0,000	1	8	0:8.00	0,003	56	212	1:11.17	0,000
44–45	9	104	1:11.56	0,000		15		0,000					9	89	1:9.89	0,000
46–47		12		0,001		1		0,317						11		0,001
48–49		1		0,317										1		
50–51		1		0,317										1		
	8041	**9255**	**1:1.15**	**0,000**	**6080**	**6963**	**1:1.15**	**0,000**	**565**	**760**	**1:1.35**	**0,000**	**1396**	**1532**	**1:1.10**	**0,000**

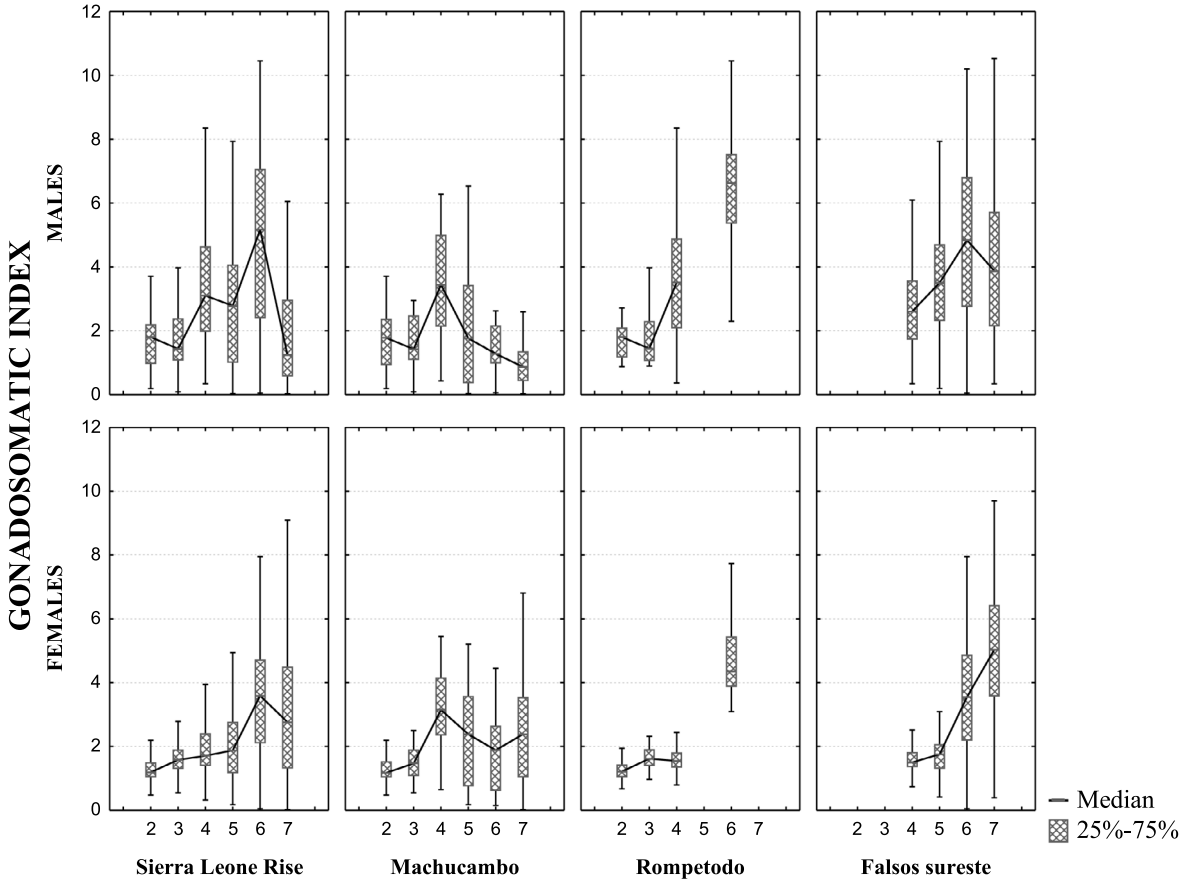

Fig. 5. Box plot (square inside the box, median, 25th to 75th percentile and I 1%–99%) of monthly variation (from February to July) of gonadosomatic index (GSI) of *Beryx splendens* in Sierra Leone Rise by sex. 2, 3, 4, 5, 6 and 7 in the abbreviations of the x axis correspond to February, March, April, May, June and July, respectively.

Table 4
Length–weight relationships ($W = aL^b$) of *Beryx splendens* in Sierra Leone Rise, (SLR), Machucambo (MA), Rompetodo (RO) and Falsos sureste (FS). N sample size; b, shape; a, allometric constant; CL, confidence limit; r^2, coefficient of determination; t is the t-test value of Student t test; GT, growth type; A-, negative allometric growth.

Seamount	Sex	LRW parameters					Student t	G T
		n	b	a	95% CL of b	r^2	t	
SLR	Both	1721	2.88	0.034	2.86–2.91	0.97	−330.7	A-
	Males	746	2.88	0.034	2.84–2.92	0.96	−236.4	A-
	Females	975	2.87	0.036	2.84–2.90	0.97	−241.7	A-
MA	Both	880	2.88	0.033	2.85–2.92	0,97	−208.9	A-
	Males	364	2.86	0.036	2.80–2.93	0.95	−154.3	A-
	Females	516	2.87	0.035	2.83–2.92	0.97	−154.0	A-
RO	Both	347	2.84	0.040	2.78–2.90	0.96	−231.9	A-
	Males	144	2.85	0.038	2.75–2.95	0.96	−153.1	A-
	Females	203	2.83	0.041	2.76–2.90	0.97	−175.2	A-
FS	Both	494	2.87	0.035	2.82–2.92	0.96	−230.3	A-
	Males	238	2.84	0.039	2.75–2.91	0.95	−177.8	A-
	Females	256	2.87	0.036	2.79–2.94	0.96	−174.7	A-

values higher than 5. However, it should be noted that for this region data were only obtained from April to July (Fig. 5).

3.5.2. Maturity

More than 90% of the *B. splendens* sampled in the Sierra Leone Rise were adults; the immature individuals represented only the 9% of the total population and they were concentrated in the month of July (4%). All stages of maturity were represented throughout the sampled months (Fig. 6). A high frequency of individuals in stage "maturing" (stage 2) was observed for males in the late winter and at the beginning of spring (February–April), with more than 50% of them in this stage. The post-spawning individuals (stage 4) represented a 10% of the total males sampled, and they did not present a clear peak through the sampling period. For females, the maximum occurrence of individuals in stage 2 was in summer (July) with a 28%, and for the stage 4 in April, reaching 40%. During the whole sampling period, spawning individuals (stage 3) were found with a clear peak in the early summer for both sexes: in July for males (43%) and in June for females (52%). Based on the GSI and macroscopic maturity stages, at least one reproductive peak occurs in summer.

In particular, in MA, spawning individuals were observed throughout the whole experimental survey (from January to July), although there was a clear increase towards the end, particularly in June for males and July for females. It is also remarkable that a large number of maturing individuals (males and females) and post-spawning (females) were found in April.

3.6. The size at sexual maturity

Based on the macroscopic scale, the size at sexual maturity (L_{50}) in the Sierra Leone Rise area was estimated at 27.80 cm (CV = 0.007) and there were no differences between sexes. Nonetheless, it was only possible to calculate the L_{50} by sex in the north (MA and FS) because in the southern seamount the number of immature individuals was very low (n = 8). As for the entire SLR, in the MA seamount there were no differences between sexes (27.7 cm; CV 0.009) but in FS females reached a larger length of L_{50} (30.64 cm; CV 0.016) than males (28.5 cm; CV 0.033) (Fig. 7; Table 5).

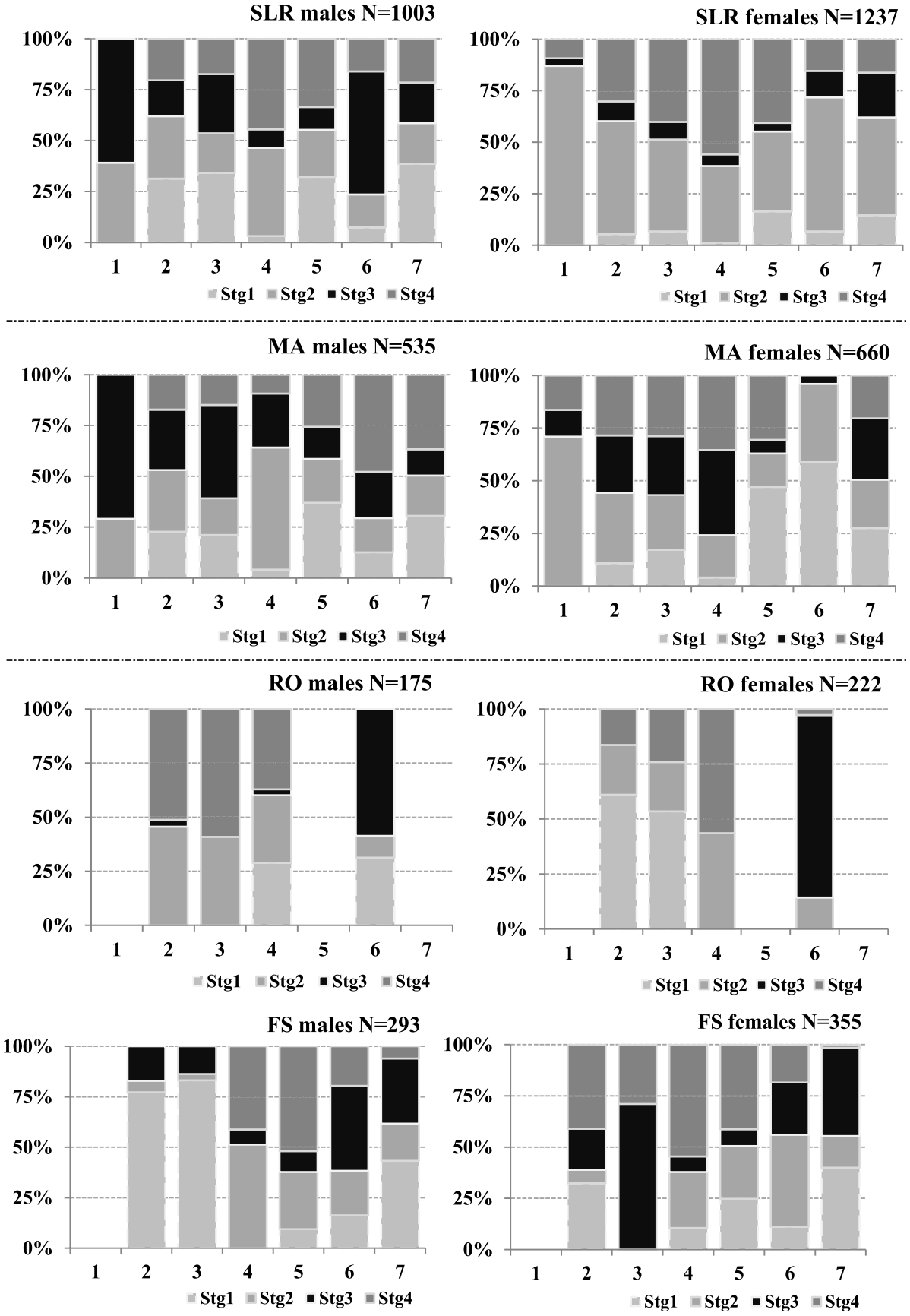

Fig. 6. Monthly variation of macroscopic mature stages of males and females of *Beryx splendens* from January (1) to July (7). Stage 1, immature, 2, maturing, 3, spawning, 4, post-spawning.

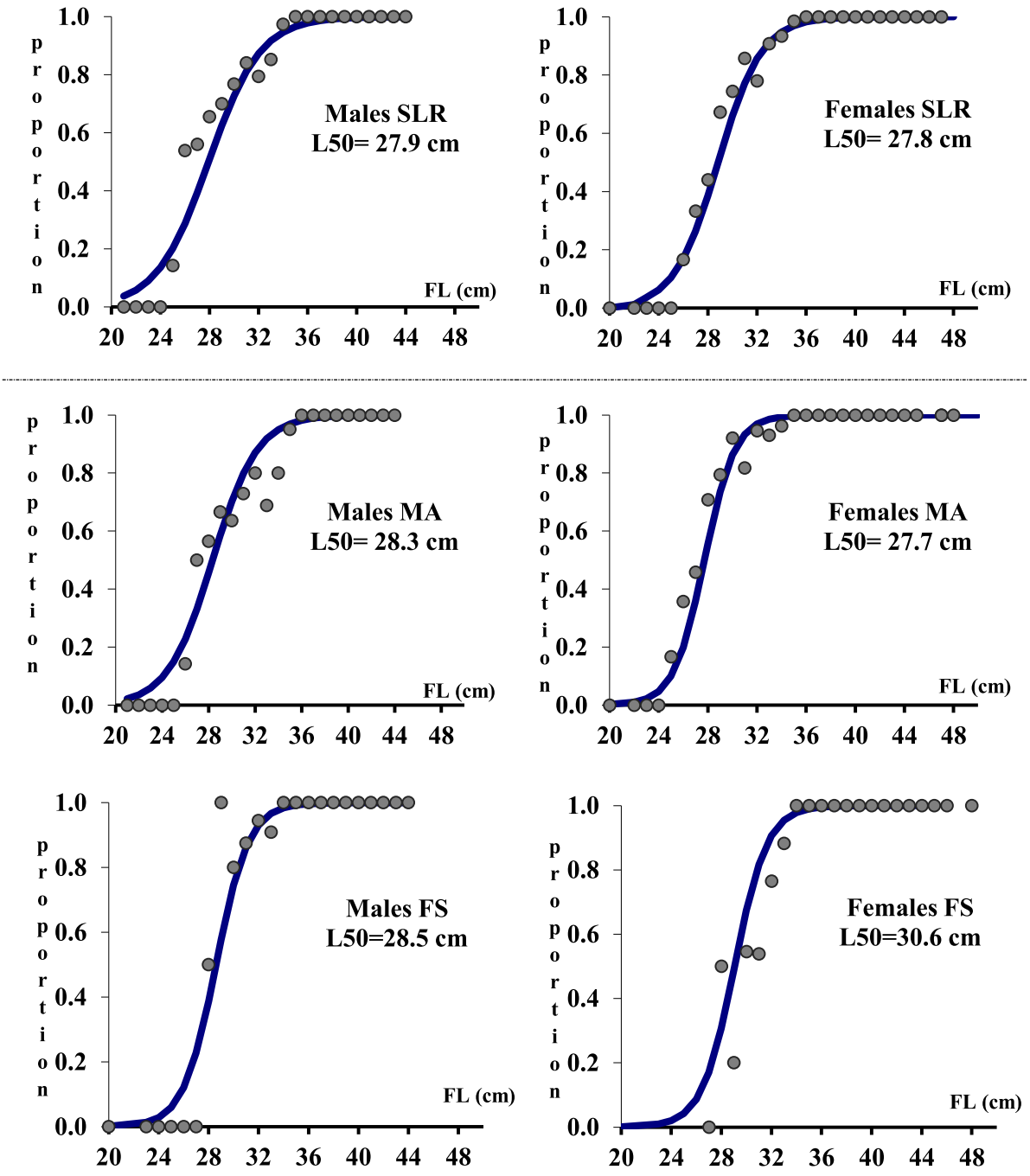

Fig. 7. Maturity ogives gives at fork length of males and females of *Beryx splendens* from the study area. Fork length estimated is indicated in the plot.

Table 5
Number of immature (Ni) and number of mature (Nm) individuals; L50 cm and CV boot in Sierra Leone Rise, SLR (MA: Machucambo; RO: Rompetodo; FS: Falsos Sureste).

	Total				Males				Females			
	Ni	Nm	L_{50}	CVb	Ni	Nm	L_{50}	CVb	Ni	Nm	L_{50}	CVb
SLR	214	2026	27.8	0.007	112	729	27.9	0.012	98	1122	27.8	0.010
MA	171	1024	27.7	0.009	100	475	28.1	0.015	71	589	27.4	0.011
RO	8	389	26.5[a]	0.069	2[a]	173	NA	NA	6[a]	216	NA	0.050
FS	35	613	29.6[a]	0.017	11[a]	239	28.5[a]	0.033	24	331	30.6[a]	0.016

[a]The number of immature is very low.

4. Dicussion

This study shows for the first time the biological parameters of alfonsino (*Beryx splendens*) from the Sierra Leone Rise. The results obtained on sex ratio, length–weight relationship, spawning season and length at sexual maturity in this study were generally similar to others authors, especially those from the Macaronesian archipelagos (Tables 6 and 7).

In all seamounts studied in Sierra Leone, alfonsino is gonochoric with no evidence of sexual dimorphism and has an unbalanced sex ratio; there were significantly more females than males. As shown in Table 6, these results are in line with findings of several authors (González et al., 2003; Pereira et al., 2012; Flores et al., 2012; McKoy et al., 2009), although other studies have demonstrated an even sex ratio (Lehodey et al., 1997) or even

Table 6
Summary of the main biological parameters of *Beryx splendens* from different areas. LWR, Length–weight Relationship (a = constant allometric and b = shape); FL, Fork Length Minimum and Maximum.

Zone	Sex ratio	LWR		FL (cm)		StudyArea
		a	b	Males	Females	
Atlantic Ocean						
Sierra Leone Rise	1:1.15	0.033	2.88	21–45	20–50	Present study
Machucambo	1:1.15	0.033	2.89	21–43	20–47	Present study
Rompetodo	1:1.35	0.039	2.83	26–42	26–43	Present study
Falsos sureste	1:1.10	0.035	2.87	27–45	27–50	Present study
Azores	1:1.21			14–36	14–42	González et al. (2003)
Azores		0.017	3.08			Leon and Malkov (1979)
Madeira	1:1.19			16–38	18–40	González et al. (2003)
Canary Island	1:1.82			24–38	28–38	González et al. (2003)
Maroc		0.081	3.10[a]	21.5–46.7[a]		Meiners-Mandujano et al. (2018)
Cape Verde Arch.		0.023	3.00[a]	26–36[a]		Pereira et al. (2012)
Pacific Ocean						
Juan Fernández, Chile	1:1.30			17–50	17–51	Flores et al. (2012)
Indian Ocean						
EEZ of Indonesia	1.55:1			12–34[a]		Satria et al. (2017)
Indian Ridge		0.038	2.98	12–55[a]		Ivanin and Rebyk (2012)
Arabian Sea	1:2.33					McKoy et al. (2009)

[a]Key: both males and females together.

Table 7
Spawning season, estimates of *Beryx splendens* FL50% and minimum and maximum fork length for mature individuals obtained by different researchers. Min FL: Minimum fork length, in cm, to the spawning stage is attained. FL50, size at which 50% of the population attain sexual maturity.

Zone	Spawning season	Min FL		FL50		StudyArea
		Males	Fem.	Males	Fem.	
Atlantic Ocean						
Sierra Leone Rise	Spring - Summer	23	25	27.9	27.8	Present study
Machucambo	Spring - Summer	23	25	27.8	28.1	Present study
Rompetodo	Spring - Summer	26	28	NA		Present study
Falsos sureste	Spring - Summer	27	28	28.5	30.6	Present study
Azores	Autumn - Winter	21	22	23.0	23.0	González et al. (2003)
Madeira	Spring	23	19	30.3	34.9	González et al. (2003)
Canary Island	Summer - Autumn	25	26	29.9	31.3	González et al. (2003)
Pacific Ocean						
Juan Fernández, Chile	Winter	33	37	36.8	39.6	Flores et al. (2012)
Juan Fernández, Chile	Winter			34.2	33.3	Guerrero and Arana (2009)
New Caledonia	Summer	33	28	34.5	33.2	Lehodey et al. (1997)
Indian Ocean						
Error Seamount				20	20.5	Kotlyar (1987)

more males than females (Satria et al., 2017). This pattern implies that some of this population experience male-biased mortality, perhaps owing to variation in predation or resource limitation. There are many examples in the literature on these biases (for example western mosquitofish, *Gambusia affinis*, Fryxell et al., 2015) and Trinidadian Guppies, *Poecilia reticulata* (McKellar et al., 2009). Moreover, these biases could also imply selectivity in the longline fishery, due to the existence of this separation of trophic strategies between males and females. Thus, Lehodey et al. (1997) found a comparable situation in males of New Caledonia. Unequal sex ratio could be related to the feeding behavior of this species in longline fisheries (Wirtz and Morato, 2001).

In spite of the sex ratio by length classes showing a high proportion of females in all sizes, in the deepest seamount, Falsos sureste (FS), males predominated in fish smaller than 38 cm (Table 3; Fig. 3). However, the number of fishes sampled from FS was only the 17% of the total; therefore, this observation from FS could be biases from the survey, combined with depth and selectivity in the longline.

The length–weight relationship of this fish species in Machucambo (MA), Rompetodo (RO) and Falsos sureste (FS) showed a parameter 'b' (shape) below 3, therefore, the growth was allometry negative for both sexes. A similar situation was pointed out for the Indian Ridge (Ivanin and Rebyk, 2012), however Leon and Malkov (1979) and Pereira et al. (2012), observed isometric growth for alfonsino in Azores; even hyperallometric growth in Maroc (Meiners-Mandujano et al., 2018). This fact could be related to the size and behavior of the individuals sampled and the summit depth of seamount in SLR because the moment of the sampling was close to the spawning season. Indeed, the depth of seamount influences environmental factors, food availability and life stage.

According to Le Cren (1951) the relative condition is an indicator of general well-being of the fish. In general, in SLR alfonsino was in a good condition and there were no significance differences between males and females in SLR and MA. However, in FS and in RO, there were significance differences in condition between males and females. As in the previous case, this could be related to the size and behavior of the individuals sampled and with the summit depth of seamounts. In general in fish, there are differential reproductive efforts and costs. Thus fish reproductive-energy output increases disproportionately with body size (Barneche et al., 2018). Hence, the big females expend more energy than males during the reproduction, and part of the sampling coincided with a spawning period.

Taking into account these results together with the GSI values, we can conclude that, at least, one reproductive period from SLR starts in April and extended at least to July. A prolonged spawning period is characteristic of highly productive environments (Tomasini et al., 1996). February was clearly a month of

reproductive rest. Flores et al. (2012), proposed that this species could show more than one pulse, but we do not have the image of the second part of the year. These results are in agreement to findings for González et al. (2003) from the Canary Islands and it could be related to the general climatic zone.

The estimates of length at sexual maturity, L_{50}, for the alfonsino in MA and FS were similar to the results reported by González et al. (2003) in the Eastern Central Atlantic (Table 7). Nevertheless, the value of L_{50} in the Sierra Leone Rise is smaller than described in the Juan Fernández Archipelago (Guerrero and Arana, 2009; Flores et al., 2012; Lehodey et al., 1997), but larger than the value found in the Indian Ocean (Kotlyar, 1987). It is known that some environmental parameters such as temperature affect fish biology (Cardinale and Modin, 1999; Brander, 1995) but the onset of maturation requires that certain conditions are fulfilled at a specific time in the life cycle (Saborido-Rey and Kjesbu, 2005) and this could explain the differences observed among areas in our study.

The population structure of *Beryx splendens* in SLR showed larger sizes for females than males and the largest specimens were found in the deepest seamounts, i.e. Falsos sureste. According to the results found in other areas, the smaller individuals were found in the shallowest seamounts, while largest individuals were found in deepest seamounts (Iguchi, 1973; Seki and Tagami, 1986; Lehodey et al., 1994). Indeed, alfonsino has a high anaerobic potential; this capacity is probably related to their ability to migrate through the oxygen minimum zone undertaking vertical migrations (Saavedra et al., 2015). The main factor of this activity has been related with the movement of its prey, which was closely related to variations in ambient sunlight and moonlight and in the oceanographic conditions of the area of seamounts (Shotton, 2016).

Alekseev et al. (1986) found a spatial segregation of alfonsino based on size and physiological condition. In seamounts of SLR, we observed mainly adults fishes in the catches, which could be related with potential bias of the selectivity effect of the longline fishery. However, many authors found similar sizes from others seamounts worldwide (Tables 6 and 7), while using different fisheries strategies. Therefore, clear differences exist in the habitat by age (Shotton, 2016). It was possible to differentiate vegetative zones from reproductive zones (fishing grounds) which are inhabited by mature individuals (Lehodey et al., 1997).

Even though genetic analyses were not undertaken in our study, in terms of genetic population structure, it is known that alfonsino is panmitic in the Northeast Atlantic waters (Aboim, 2005). Alfonsino can migrate from mount to mount over long distances across the oceans (Lévy-Hartmann et al., 2011), although, alfonsino does not occur above a depth of 200 m and alfonsino requires a close proximity between seamounts (Quéro et al., 1990, Maul 1981). Probably, seamounts may serve to encourage the migration of the species, as stopping points in their migration and supporting connectivity between distant marine populations (Parsons, 1996; Williams and Benzie, 1998; Shulman and Bermingham, 1995; Shulman, 1998). However, in our study we found that this species spawns around the Sierra Leone Rise. Furthermore, there is no single record on mature alfonsino migrations in the open ocean (Kotlyar, 1987). Therefore, since there are reproductive adults in SLR, and that the pelagic phases could travel long distances, we concluded that SLR could be a relevant refuge area, and dispersal origin of new recruits toward areas already under fishery pressure around the Central-Western African Coast.

According to Hilborn and Hilborn (2012), all fish stocks are susceptible to be fished, but the maximum sustainable yield that can be exploited will depend on the degree of resilience of the population, as well as the vulnerability of overfishing in the area. Therefore, a previous assessment is crucial to establish the resilience capacity of the stock. Salmerón et al. (2015), observed a rapid depletion due to the fishing pressure. Altogether, we do not recommend fishing in this area until further prospecting and evaluating the levels of alfonsino resilience from the Sierra Leone Rise.

The main weakness of the present study is that we do not have the complete image of the whole year, due to the fact that samples only came from 7 months (January–July). However, these are the only data available for SLR. Future studies could increase our knowledge of population resilience 20 years after the experimental fisheries survey was carried out by IEO from SLR, and complete the annual period shown in current study, and to give to us a complete picture of the alfonsino annual cycle. Nevertheless, the current paper shows a basic and valuable baseline for future studies.

CRediT authorship contribution statement

Francisca Salmerón: Conceptualization, Methodology, Investigation, Resources, Formal analysis, Writing – original draft, Editing review. **Elena Barcala:** Investigation, Writing – review, Resources. **Lourdes Fernandez-Peralta:** Resources. **Javier Rey:** Resources. **José C. Báez:** Writing – review & editing, Investigation, Validation, Supervision, Resources, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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